

BIOGEOGRAPHIC PATTERNS IN FLIGHT CAPACITY OF NEARCTIC GRASSHOPPERS (ORTHOPTERA:ACRIDIDAE)¹

Daniel Otte²

ABSTRACT: The North American species of Gomphocerinae and Acridinae display several interesting biogeographic trends. The proportion of obligately flightless species increases southwards towards the tropics and westwards from the central prairies to the Pacific coast, and is also higher on islands. Facultative nonflying species are unknown in Central America and the Caribbean region and are most common in northern and northeastern parts of the United States. Species ranges are smallest for obligate nonflyers, while obligate flyers and facultative flyers do not differ significantly.

While preparing a handbook on the North American grasshoppers, all described valid species of slant-faced grasshoppers (Gomphocerinae and Acridinae) from Panama northwards and the Caribbean region were studied and their ranges plotted. Several interesting biogeographic patterns and trends relating to condition of flight were noticed and are reported here. Unfortunately the number of species involved is not large enough in most comparisons to indicate that the differences observed are statistically significant. The species examined are listed in Table 1 along with the geographic center of their ranges, the estimated size of their ranges and whether or not they can fly. Distribution areas were estimated by placing a grid (176 km to a side) over a distribution map and counting the squares which included a part of the species range.

(1) Roughly 48% of the species are *obligate flyers*, species in which both sexes are always capable of flight during some part of their adult life (here called *F-species*). Approximately 18% are *facultative flyers*, species in which at least one sex or some individuals of either sex are capable of flight (*f-species*). The remaining 37% are *obligate nonflyers*, species in which flying or long-winged individuals have not been found (*N-species*). Flying ability in both *F-* and *f-species* varies considerably; some species are capable of flying up to 50 m or more when disturbed (*Rhammatocerus* and *Mermiria* species), others can fly a few meters at most (*Parapomala*).

(2) The *f-species* category includes the following combination of flying and nonflying individuals: (a) both sexes are usually capable of flight, but in some geographic regions they are flightless (e.g., *Amphitornus coloradus*, *Ageneotettix deorum*, *Horesidotes cinereus*, and *Opeia obscura*); (b) males are capable of flight but females are usually not (e.g., *Aeropedellus clavatus*); (c) both sexes are usually unable to fly, but occasional individuals are long-winged and capable of flying (e.g., *Chorthippus curtipennis*, *Dichromorpha elegans*) and *D. viridis*, *Chloealtis conspersa* and *C. abdominalis*, and *Boopedon nubilum*).

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²Department of Entomology, Academy of Natural Sciences, Philadelphia, Pennsylvania, 19103.

(3) The forewings of males are usually longer than those of females. The reason seems to be that males in this group use their forewings in stridulating and retain them principally for this reason. In only one species is the male apparently capable of flight and the female unable to fly (*Aeropedellus clavatus*).

(4) On the continent the proportion of *N-species* decreases northwards and is significantly lower in regions A, B, and C (Fig. 1) than in regions H (X^2 test: $p < .05$, $df = 1$). Moving from region H to A in the central part of the continent, percentages of *N-species* decrease as follows: Central America 56%, southern Mexico 33%, northern Mexico and SW United States 15%, central prairies 8%, northern prairies 12%. Differences among regions A, B, C, and E are not significant (X^2 tests); but the difference between regions A or C and G are significant at the 0.1 level. Along an eastern transect the trend is similar: Caribbean regions 67%; Florida and SE United States 14%, NE United States 0%.

(5) The proportion of *f-species* decreases southwards. Through the center of the continent region A has 24% *f-species*; regions B and E have 15%; region G has 11% and region H has 0%. In southern Mexico, Central America and the Caribbean region the Gomphocerinae can either fly or they cannot.

(6) Along the east-west transect through the United States the west has a higher proportion of *N-species* than the east, but the proportion of *f-species* is higher in the east than the west. However, this is a trend and the difference is not statistically significant at the 0.05 level.

(7) High altitude populations of a species are more likely to be flightless than low altitude populations. Among the Gomphocerinae the pattern is seen only in *Amphitornus coloradus* and *Ageneotettix deorum*. The flightless populations of *Ageneotettix deorum* are known only from higher elevations in Arizona and Colorado, and the short-winged form of *Amphitornus coloradus* has been collected only at higher elevations in the Tushar Mountains in Utah and in the San Francisco Mountains and Kaibab Plateau in Arizona.

(8) *N-species* have smaller ranges on the average than either *f-species* or *F-species*. This trend is evident in frequency histograms in Fig. 1. Interestingly, *F-species* and *f-species* do not differ significantly in range size.

Many of the short-winged and flightless species of grasshoppers in Central America are associated with forests, forest openings and forest margins, or mountain ridges. The ranges of most of them are small when compared to those of flying species from the same region, so the small ranges appear to be a direct consequence of their flightlessness and not due to the relatively constricted land mass. The cause of flightlessness in Central America and the Caribbean may be a greater stability of habitats and hence reduced selective pressures for dispersability. Alternatively, the species tend to be restricted to islands or islands of suitable habitat within forests and may be subject to some of the same pressures promoting winglessness on oceanic islands. With loss of flight and the consequent

reduction in vagility, isolated populations are less likely to exchange genetic material over the longer term, and thus may speciate more rapidly. Because the ranges of many of the Central American species are very restricted, I believe it is likely that many more species will be discovered when forest and mountain habitats are more thoroughly explored, and this will further

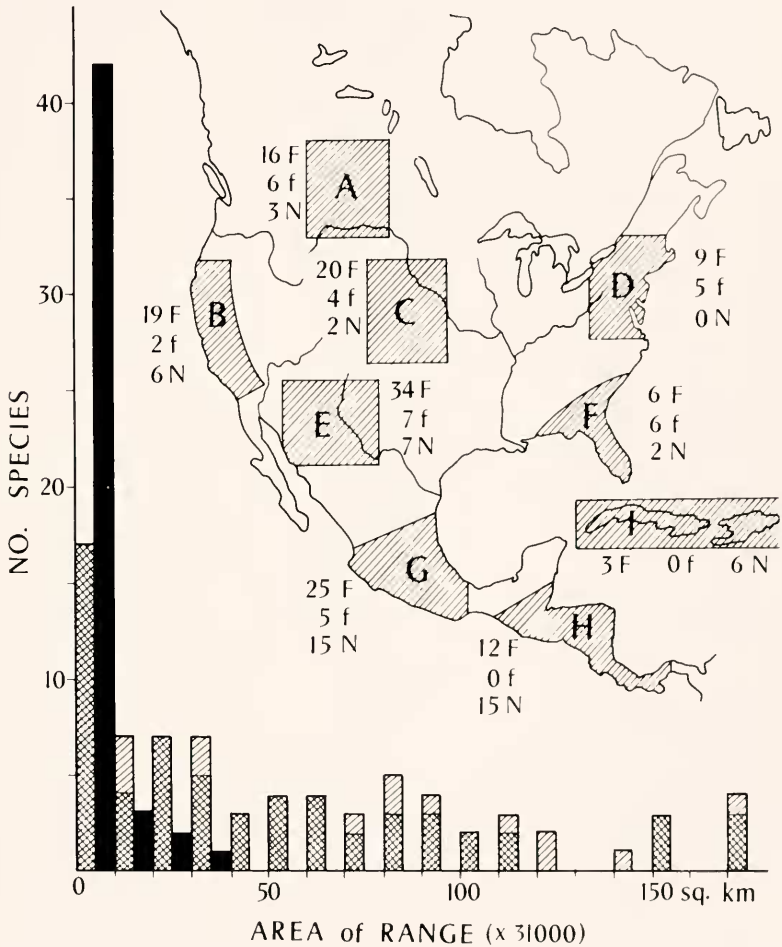


Fig. 1. The map shows areas compared for numbers of F-, f-, and N-species. Proportions of these categories differ significantly between region H and regions A, B, C, and E. The frequency histogram illustrates that relatively many more N-species (black) have small ranges, and none have large ranges. Mean range size of f-species (hatched) and F-species (cross-hatched) do not differ significantly ($P < 0.05, X^2$ test).

increase the proportion of flightless species. Some of the flying species in Central America are most common in weedy and disturbed habitats leading one to wonder if the number of flying species is now higher than it was prior to human disturbance.

Table 1. List of species included in this survey, along with range size and functional condition of wings. F, capable of flight; N, unable to fly. The / separates the condition of males on the left and females on the right. When / is absent both sexes are alike. Parentheses indicate the rare condition: Example: F.N./F(N) indicates flying and nonflying males are both common, but that nonflying females are uncommon.

	Approximate center of range	Estimated range size (sq km)*	Flight
<i>Acantherus piperatus</i>	New Mexico	25	F
<i>Achurum carinatum</i>	Florida	20	N
<i>Achurum minimipenne</i>	NE Mexico	7	N
<i>Achurum sumichrasti</i>	C Mexico	40	F
<i>Acrolophitus hirtipes</i>	Colorado	74	F
<i>Acrolophitus nevadensis</i>	N Arizona	9	F
<i>Acrolophitus maculipennis</i>	No. Mexico	30	F
<i>Acrolophitus pulchella</i>	Idaho	<1	F
<i>Aeropedellus clavatus</i>	Montana	80	f/N
<i>Ageneotettix brevipennis</i>	No. Mexico	9	N
<i>Ageneotettix deorum</i>	Colorado	188	F(N)
<i>Ageneotettix salutator</i>	NW Mexico	16	F-N
<i>Amblytropidia elongata</i>	C Mexico	15	F
<i>Amblytropidia mysteca</i>	E Texas	86	F
<i>Amblytropidia trinitatis</i>	Panama	20++	F
<i>Amphitornus coloradus</i>	Colorado	144	F(N)
<i>Amphitornus durangus</i>	W Mexico	2	F
<i>Aulocara brevipenne</i>	No. Mexico	2	N
<i>Aulocara elliotti</i>	Colorado	156	F
<i>Aulocara femoratum</i>	Colorado	95	N(F)
<i>Boopedon auriventris</i>	Kansas	17	N
<i>Boopedon dampfi</i>	S Mexico	6	N
<i>Boopedon diabolicum</i>	C Mexico	7	N
<i>Boopedon empelios</i>	W Mexico	1	N
<i>Boopedon flaviventris</i>	W Mexico	18	N
<i>Boopedon gracile</i>	Texas	34	F/N(F)
<i>Boopedon nubilum</i>	Colorado	75	N(F)/N(F)
<i>Boopedon rufipes</i>	C Mexico	6	N
<i>Boottettix argentatus</i>	No. Mexico	44	F
<i>Boottettix joerni</i>	No. Mexico	3	F
<i>Chiapacris eximius</i>	C Mexico	1	N
<i>Chiapacris nayaritus</i>	W Mexico	1	N?
<i>Chiapacris velox</i>	S Mexico	3	F
<i>Chloealtis abdominalis</i>	Montana	57	N(F)/N(F)
<i>Chloealtis aspasma</i>	NW USA	1	N
<i>Chloealtis conspera</i>	Minnesota	114	N(F)/N(F)

	Approximate center of range	Estimated range size (sq km)*	Flight
<i>Chloeahtis diana</i>	N California	5	N
<i>Chloeahtis gracilis</i>	S California	6	N?
<i>Chorthippus curtippennis</i>	North Dakota	250+	N.F./N.F
<i>Chrysochraon petraea</i>	NW USA	3	N
<i>Cibolacris crypticus</i>	W Mexico	5	F
<i>Cibolacris parviceps</i>	S Arizona	51	F
<i>Cibolacris samalayuca</i>	No. Mexico	2	F
<i>Compsacrella poecila</i>	Cuba	1	N
<i>Cordillacris crenulata</i>	Colorado	67	F
<i>Cordillacris occipitalis</i>	Colorado	90	F
<i>Dichromorpha elegans</i>	SE USA	33	N(F)
<i>Dichromorpha prominula</i>	W Mexico	16	F
<i>Dichromorpha viridis</i>	Misissippi	125	N(F)
<i>Eritettix abortivus</i>	Texas	22	N
<i>Eritettix obscurus</i>	Florida	6	N
<i>Eritettix simplex</i>	Iowa	115	F
<i>Esselenia vanduzeei</i>	C California	3	N
<i>Eupnigodes megacephala</i>	C California	5	N
<i>Eupnigodes sierranus</i>	C California	7	F
<i>Heliaula rufa</i>	New Mexico	31	F
<i>Horesidotes cinereus</i>	S Arizona	14	F(N)
<i>Horesidotes deiradonotus</i>	W Mexico	2	N(F?)
<i>Leurohippus stoneri</i>	Antigua	<1	N
<i>Ligurotettix coquilletti</i>	W Arizona	22	F
<i>Ligurotettix planum</i>	No. Mexico	17	F
<i>Melanotettix dibeloni</i>	C Mexico	4	N
<i>Mermiria bivittata</i>	Oklahoma	95	F
<i>Mermiria intertexta</i>	SE USA	17	F
<i>Mermiria picta</i>	E Texas	83	F
<i>Mermiria texana</i>	W Texas	35+	F
<i>Metaleptea brevicornis</i>	C America	200+	F
<i>Opeia obscura</i>	Colorado	127	F(N)
<i>Opeia atascosa</i>	W Mexico	6	N
<i>Orphula azteca</i>	C America	24	F
<i>Orphula vitripenne</i>	Yucatan	2	F
<i>Orphulina balloui</i>	C America	20+	F
<i>Orphulella aculeata</i>	C Mexico	4	F
<i>Orphulella brachyptera</i>	Cuba	1	N
<i>Orphulella concinnula</i>	South America	150+	F
<i>Orphulella decisa</i>	Caribbean	1	N
<i>Orphulella losamatisensis</i>	N South America	50+	F
<i>Orphulella nesicos</i>	Caribbean	1	N
<i>Orphulella orizabae</i>	C Mexico	6	F
<i>Orphulella pelidna</i>	Nebraska	200+	F
<i>Orphulella pernix</i>	Costa Rica	1	N

	Approximate center of range	Estimated range size (sq km)*	Flight
<i>Orphulella punctata</i>	N South America	150+	F
<i>Orphulella quiroga</i>	C Mexico	7	N(F)
<i>Orphulella scudderii</i>	Cuba	4	F
<i>Orphulella speciosa</i>	Missouri	110	F
<i>Orphulella tolteca</i>	C Mexico	4	F
<i>Orphulella trypha</i>	Caribbean	1	N
<i>Paropomala wyomingensis</i>	New Mexico	65+	f
<i>Paropomala pallida</i>	Arizona	55	f
<i>Paropomala virgata</i>	New Mexico	22	F
<i>Phaneroturris cupidus</i>	C America	2	N
<i>Phaneroturris tantillus</i>	C America	1	N
<i>Phlibostroma quadrimaculatum</i>	Kansas	80+	f
<i>Prorocorypha snowi</i>	NW Mexico	3	N
<i>Psoloessa brachyptera</i>	C Mexico	2	N
<i>Psoloessa delicatula</i>	Colorado	111	F
<i>Psoloessa meridionalis</i>	C Mexico	14	N(F)
<i>Psoloessa microptera</i>	NE Mexico	2	N
<i>Psoloessa texana</i>	W Texas	95	F
<i>Pseudopomala brachyptera</i>	S Dakota	85	N.F
<i>Rhammatocerus viatorius</i>	S Mexico	33+	F
<i>Rhammatocerus cyanipes</i>	N South America	20	F
<i>Silvitettix aphelocoryphus</i>	C America	1	N
<i>Silvitettix audax</i>	C America	1	N
<i>Silvitettix biolleyi</i>	C America	3	N
<i>Silvitettix chloromerus</i>	C Mexico	3	N
<i>Silvitettix communis</i>	C America	2	N
<i>Silvitettix gorgasi</i>	C America	1	N
<i>Silvitettix maculatus</i>	C America	6	N
<i>Silvitettix rhachicoryphus</i>	S Mexico	2	N
<i>Silvitettix ricei</i>	S Mexico	1	N
<i>Silvitettix salinus</i>	S Mexico	2	N
<i>Silvitettix thalassinus</i>	C America	10	N
<i>Silvitettix whitei</i>	S Mexico	1	N
<i>Stenobothrus brunneus</i>	Montana	42	F
<i>Stenobothrus shastanus</i>	Oregon	35	N
<i>Stethophyma gracile</i>	Minnesota	60	F
<i>Stethophyma lineata</i>	Minnesota	60+	F
<i>Stethophyma celata</i>	Iowa	30+	F
<i>Syrbula admirabilis</i>	E Texas	100+	F
<i>Syrbula festina</i>	S Mexico	6	F
<i>Syrbula montezuma</i>	No. Mexico	73	F
<i>Xeracris minimus</i>	S California	8	F
<i>Xeracris snowi</i>	W Arizona	7	F

*x 31,000